

THE UNIVERSITY OF KANSAS
PALEONTOLOGICAL CONTRIBUTIONS

July 22, 1977

Paper 87

MAGNESIUM CONTENT OF CALCITE IN CARAPACES
OF BENTHIC MARINE OSTRACODA¹

H. MEADE CADOT, JR.,² and ROGER L. KAESLER³

² Antioch College—New England and The Harris Center for
Conservation Education, Hancock, New Hampshire;

³ The University of Kansas, Lawrence

ABSTRACT

Statistically significant differences in mean magnesium content of calcite in carapaces of benthic marine Ostracoda were found to occur among four superfamily groups and among regions of the carapace for each of the superfamily groups. For the Ostracoda studied, the mean composition was 3.5 mole percent MgCO_3 . The Cypridacea had the highest mean value, 5.2 mole percent MgCO_3 ; whereas the mean for the Cytheracea was much less, 1.9 mole percent MgCO_3 . The means found for the other two groups, the Bairdiacea and the Cytherellidae, were both about 4.3 mole percent MgCO_3 . The inner region of the carapace was found to contain the most magnesium in all four superfamily groups, the mean ranging from 2.1 mole percent MgCO_3 for the cytheraceans to 6.2 mole percent MgCO_3 for the cypridaceans.

Phylogenetic control of magnesium was judged to be important at both the class and superfamily levels. That members of Class Ostracoda substitute magnesium for calcium in calcite may be partially explained by the fact that all ostracodes, in order to survive, must calcify their carapaces rapidly following molting. Furthermore, it would seem advantageous that the most rapid calcification take place in that portion of the carapace immediately adjacent to the soft anatomy. If so, differences in magnesium content among carapace regions might be the result of this difference in calcification rate. The reason for the significant difference in magnesium content among superfamily groups is not known but may be due to the fact that the cytheraceans are more highly evolved than the other groups studied.

Variation of water temperature was judged to be a significant source of variation in magnesium content at the superfamily level, independent of rate of growth. Rank correlations between magnesium concentration and temperature averaged about 0.7 for the four superfamily groups, with the cytheraceans showing the best correlation (0.78). Depth, independent of temperature, was judged not to be an important factor. Depth was imperfectly correlated with temperature and was not as highly associated with magnesium content as was temperature.

¹ Manuscript received December 23, 1976; revised manuscript received March 22, 1977.

INTRODUCTION

The dominant form of calcite precipitated in benthic marine environments is magnesium calcite, most of which is biogenic. Although non-skeletal magnesium calcite is known to occur in deep-sea and intra-reef environments (Friedman, Amiel, & Schneidermann, 1974), synthesis of inorganic magnesium calcite in the laboratory has not been achieved except by using solutions with salt concentrations unknown in open, euhaline environments. Natural carbonates are in poor agreement with thermodynamic theory (Cloud, 1965), and Moberly (1968) has suggested that we should search among organic mineralization processes for the explanation of these phenomena.

Wet-chemical analyses by Clarke and Wheeler (1922) and X-ray diffraction analyses by Chave (1954) indicated that magnesium content in skeletal calcite is positively correlated with water temperature. These results have been cited often in the literature (for example, Revelle & Fairbridge, 1957; Lowenstam, 1963; Dodd, 1967; Wolfe, Chilingar, & Beales, 1967; Bathurst, 1971; Blatt, Middleton, & Murray, 1972; Lippmann, 1973; Milliman, 1974). Chave also suggested that his data indicated phylogenetic control of the magnesium content of calcite. He believed that phyla considered more advanced might be better able to discriminate against magnesium during precipitation of calcite. Blatt, Middleton, and Murray (1972) suggested that magnesium causes a structural defect in the calcite crystal lattice, but Dodd (1967) concluded that exclusion of magnesium in the calcification process is without obvious selective advantage. Furthermore, Dodd noted that some advanced groups studied by Chave had too much magnesium for their assumed phylogenetic level, including ostracodes, decapods, and echinoderms. Moberly (1968) used an electron microprobe to study calcite of coralline algae and bivalves from temperate localities where there is seasonal temperature change. His data indicated that growth rate might be the key to magnesium control and that rapidly growing organisms are less able to discriminate against magnesium during shell construction. If this is true, it may well explain why ostracodes and decapods contain more magnesium than it appears they should. Ostracodes and decapods (but not

echinoderms) grow by molting, and individuals must calcify to varying degrees rapidly after molting in order to survive. Moberly (p. 79) concluded that temperature was "of decidedly less overall significance"; however, he pointed out that the effects of other factors such as light, salinity, and reproductive cycles have not yet been determined experimentally and that generalizations, including his own, need to be tested on a wide variety of organisms. Davies, Crenshaw, and Heatfield (1972) concluded from a study of echinoid spines that temperature is not an independent factor in control of magnesium but merely affects rate of growth.

For several reasons ostracodes are excellent organisms for studying the effects of phylogeny, temperature, and depth on magnesium concentration in calcite.

1) Ostracodes are found throughout the normal marine environmental spectrum from high latitudes to the tropics and from intertidal to abyssal depths. (Our study deals primarily with marine species.)

2) Relative to the photosynthetic coralline algae studied by Moberly (1968), light is much less of a factor.

3) Variation in rate of growth of the animal can be regarded as an insignificant factor in explaining variations in magnesium content of Ostracoda. Ostracodes grow discontinuously by ecdysis with calcification occurring just after molting, so that growth rate determines when and how often new calcification takes place but not necessarily how fast it takes place. Furthermore, because rapid calcification following molting is essential for survival, water temperature is probably unimportant, and calcification is nearly instantaneous when compared with other organisms.

4) Unlike coralline algae, bivalves, and echinoderms, variations of calcite within the carapace precipitated by a single ostracode cannot be attributed to seasonal changes in water temperatures. The calcite of ostracodes can only reflect the ambient temperature immediately following the time of molting. Molting takes place every few days or weeks, so that if specimens living at the time of collection are studied, their calcite

closely reflects the water temperature at the time of collection, thus making them ideal for the study of correlation between temperature and magnesium content. It is possible that the close correspondence holds only for the early instars because of the long adult life of some species. Nevertheless, Van Morkhoven (1962) has pointed out that freshwater species can go through as many as three generations in a single summer, individuals of each generation molting nine times. If so, the time lapse between molts would average four days or less.

5) Phylogenetic control of magnesium content within orders of living ostracodes can be assessed because species belonging to different suborders and superfamilies are found together in many ostracode communities regardless of temperature and depth of environment.

Chave's pioneer survey (1954) included some X-ray diffraction analyses of ostracode calcite but only of a few shallow-water samples. Techniques of analysis have been improved during the past 23 years, so that it is now possible to go beyond Chave's beginning. He was unable to determine accurately magnesium content in samples containing less than four mole percent magnesium carbonate, which included half of his ostracode samples. Futhermore, Milliman, Gastner, and Müller (1971) challenged Chave's choice of lattice constant versus composition curve and suggested his estimates of magnesium content were too high.

A pilot study was undertaken to demonstrate that electron microprobe techniques could be successfully applied to the study of ostracodes (Cadot, Van Schmus, & Kaesler, 1972; Cadot, Kaesler, & Van Schmus, 1975). (Lipps and Ribbe in 1967 reported that electron microprobe analysis of planktonic Foraminiferida was difficult because of the porous nature of the tests.) Results of the pilot study indicated Chave's estimates of magnesium content of calcite in ostracodes might be too high, as suggested by Milliman, Gastner, and Müller (1971). Other important findings from the study were:

1) Phylogenetic line might be an important control of magnesium concentration within the Class Ostracoda. Chave was unable to assess phylogenetic control within Ostracoda because his samples each contained more than one species,

and species were mixed without regard to higher taxonomic category.

2) Temperature may exert control, but correlation between temperature and magnesium concentration was low when means of temperature and magnesium content were plotted for all specimens regardless of taxonomy.

3) Variation within an individual ostracode is sometimes greater than variation among individuals of the same species and from the same locality. Chave was unable to study variation within individuals because his samples were crushed and contained many individuals.

These results from the pilot study led to the following hypotheses to be investigated in this research:

1) Phylogenetic control of magnesium in calcite extends at least to the superfamily level; and, therefore, the magnesium content of ostracodes of different superfamilies but from the same environment should be significantly different.

2) Variation within individual carapaces is a significant source of variation in the magnesium content of ostracodes; that is, magnesium content differs significantly among inner, middle, and outer regions of the carapace even when specimens are drawn from the same environment and belong to only one taxonomic group.

3) Contrary to the results of the pilot study, when enough data are examined, magnesium content of Ostracoda at the class level would show close correlation with water temperature as suggested by Chave (1954).

4) Temperature is closely correlated with depth, but depth does not represent a *separate* source of variation of magnesium within Ostracoda.

These hypotheses were tested by using electron microprobe analysis to determine the magnesium content of representatives of the four major groups of benthic marine Ostracoda collected from environments with a wide variety of water temperature and depth. Statistical analysis of the resulting data was then used to determine whether statistically significant differences in mole percent MgCO_3 existed within carapaces and among carapaces of ostracodes belonging to different superfamily groups and whether these differences were correlated with differences in water temperature and water depth.

ACKNOWLEDGMENTS

We are grateful to W. R. Van Schmus, Wakefield Dort, Jr., R. H. Benson, M. J. Brady, R. M. Forester, A. J. Rowell, and P. S. Humphrey, who provided helpful comments on the contents of the manuscript. We also wish to acknowledge the assistance of the following people during various phases of the study: W. R. Van Schmus for arranging for our use of the electron microprobes at the Smithsonian Institution and at the Virginia Polytechnic Institute and State University; R. H. Benson for sponsoring Cadot's summer internship at the Smithsonian Institution; Kurt Boström, chief scientist, and the crew of *Eltanin* Cruise 39, and Henry Imshaug, chief scientist, and the crew of *Hero* Cruise 71-5 for valuable assistance in obtaining deep-sea and high-latitude, cold-water ostracode samples; Gene Jarosewich for arrangements for and Charley Obermeyer and Joe Nellen for their assistance in obtaining microprobe analyses at the Smithsonian Institution; Paul Ribbe for

arrangements for and Tim Kurtz for assistance in obtaining microprobe analyses at the Virginia Polytechnic Institute and State University. For supplying us with supplemental ostracode material, we thank F. M. Swain, P. R. Krutak, R. H. Benson, J. T. Durazzi, and M. D. Brondos.

Financial support for the study was received from the following sources: National Science Foundation Grants GA-12472 and GV-25157 to The University of Kansas; National Science Foundation Grant GB-4446, for travel to and support at the Bermuda Biological Station and travel to the Florida Keys; and the Geological Society of America, for a research grant to Cadot to cover expenses for microprobe analyses at the Virginia Polytechnic Institute and State University. General financial support was provided by the Department of Geology of The University of Kansas, the Smithsonian Institution, and the Shell Oil Company.

MATERIALS AND METHODS

CHOICE OF SPECIMENS FOR STUDY

Most of the material studied was drawn from collections made by the authors and has been deposited in the University of Kansas Museum of Invertebrate Paleontology (KUMIP numbers 1,046,006 to 1,046,271). Shallow-water, tropical specimens were collected in Bermuda and the Florida Keys. Shallow-water temperate specimens were collected from the coasts of southern Maine and southern Victoria, Australia. Shallow, cold-water, high-latitude specimens were obtained during cruise 71-4 of the RSV *Hero* to Isla de los Estados (east of Isla Grande, Tierra del Fuego). Deep-sea, cold-water specimens were collected during Cruise 39 of the *Eltanin* to the southern Indian Ocean and the Tasman Sea. Some supplemental material was also obtained from the following sources: M. J. Brady (University of Kansas), R. H. Benson (Smithsonian Institution), F. M. Swain (University of Minnesota and University of Delaware), and P. R. Krutak (University of Nebraska). All stations sampled are listed in Appendix I of Cadot (1974).

None of the specimens considered for study showed any signs of recrystallization, but this

alone does not insure lack of alteration. The results of the pilot study indicated that carapaces may sometimes lose magnesium after death of the animal without showing any signs of recrystallization. Examples are given in Appendix III, Table 1, of Cadot (1974). Loss of magnesium without noticeable recrystallization has been documented for other organisms including coralline algae and echnioids (Moberly, 1973; MacQueen, Ghent, & Davies, 1974). It is possible that pairs of Mg^{2+} and CO_3^{2-} ions may leave the calcite by what Land (1967) called incongruent dissolution, while the primary Ca^{2+} and associated CO_3^{2-} ions, which make up more than 90 percent of the carapace, remain as a permanent solid framework (Land, 1967). Schroeder (1969) suggested that this process can take place in submarine as well as subaerial environments, although the mechanism is not well understood (Bathurst, 1971). The exact postmortem time lapse before such magnesium loss takes place is not known, but it probably does not occur prior to decomposition of soft parts, which may take place in as little as 72 hours (R. M. Forester, pers. commun.). Moberly (1973) noted that the first detectable change in high-magnesium calcite of coralline algae oc-

curred three to 10 years after the death of the plant.

Material selected for this study included only those specimens that still contained soft parts and were alive at or just prior to the time of collection, thereby minimizing the likelihood of loss of magnesium. This considerably reduced some of the sample sizes, particularly those from deep-sea environments, but deep-sea specimens are probably the most susceptible to early diagenetic changes (Friedman, 1965). Most of the supplemental material consisted of dry specimens, but the specimens used contained at least some vestige of soft parts.

Material studied included representatives of the three marine superfamilies of Suborder Podocopina and the one extant family in the Suborder Platycopina. Because the family Cytherellidae is the only family in Suborder Platycopina, no superfamily name exists, and cytherellids have not been referred to in the literature as cytherellaceans. However, in this research the Cytherellidae have been referred to as a taxonomic group of superfamily rank for the sake of parallelism and to emphasize the fact that they do not belong to any of the three podocopine superfamilies. The three podocopine superfamilies plus the platycopine family will henceforth be referred to as the *four superfamily groups*. The suprageneric classification used was taken from the *Treatise of Invertebrate Paleontology* (Moore, 1961) and was used according to more recent information summarized by Maddocks (1972) (see Table 1).

TABLE 1. *Suprageneric Classification of the Ostracoda Studied in This Research* (from Moore, 1961).

| |
|------------------------|
| Subclass Ostracoda |
| Order Podocopida |
| Suborder Platycopina |
| Family Cytherellidae |
| Suborder Podocopina |
| Superfamily Bairdiacea |
| Superfamily Cypridacea |
| Superfamily Cytheracea |

It is quite possible that salinity or ionic ratios may exert some control of magnesium content of calcite. Analyses in a pilot study of *Cypridopsis vidua* from fresh water showed much lower concentrations of magnesium than would be ex-

pected in normal marine cypridaceans from environments with similar temperature (Table 2) (see also Crisp, 1972, and Durazzi, 1973). It is hoped that the effect of salinity was minimized in this study by using only those specimens collected from normal marine (euhaline) environments, although this still included a fairly wide range of salinities (probably 30 to 37 but possibly 30 to 39 parts per thousand).

TABLE 2. *Comparison of Fresh Water Cypridopsis vidua with Euhaline Cyprididae.*

| | Temperature, °C | Number of Analyses | Mean of Mole % MgCO ₃ |
|--------------------------|-----------------|--------------------|----------------------------------|
| Euhaline Cyprididae | 13-17 | 116 | 5.14 |
| <i>Cypridopsis vidua</i> | 24.4 | 24 | 1.33 |
| Euhaline Cyprididae | 24-26 | 154 | 7.49 |

ELECTRON MICROPROBE ANALYSIS

Microprobe analysis offers several advantages over other methods of analysis for study of ostracodes (Cadot, Kaesler, & Van Schmus, 1975). The technique does not require specimens to be crushed or dissolved and makes it possible both to examine variation within a single specimen and to avoid contamination by non-carbonate magnesium. Analytical error in this study was held to ± 10 percent and probably to ± 5 percent. Errors as low as ± 1 percent are possible in some microprobe analysis; however, this is probably not possible for analysis of calcite since it is less stable under the electron beam than other minerals, such as dolomite and magnesite. Nevertheless, by employing a relatively large beam diameter (6 to 8 μ) and by restricting counting time during exposure to the beam to 10 seconds, accelerating voltage to 15 kilovolts, and beam current to 0.15 milliamps, error due to thermal decomposition was held to within 2.5 percent. The calibration curve used was essentially linear so that error due to curvilinearity was probably less than one percent.

The basic principle of microprobe analysis is relatively simple. A beam of electrons, focused to a few microns in diameter, impinges on the flat, polished surface of a specimen. Atoms under the beam are thus excited and emit X rays that are characteristic of each element. These X rays are dispersed according to wave length by crystal spec-

trometers and counted by use of the appropriate detector.

Sample preparation for analysis was by far the most taxing activity and, aside from the oceanographic cruises, the most time-consuming activity because the ostracodes were small (0.5 to 2.0 mm) and brittle. Nearly three hundred specimens were prepared on which a total of more than five thousand analyses were performed. To our knowledge, this is the most extensive study of skeletal calcite yet undertaken using electron microprobe analysis.

The preparation was as follows: One of the two valves of a carapace was removed from each specimen and mounted with epoxide on a glass disk cut to fit a microprobe sample holder (2.5 cm diameter). The specimens were then embedded with a second application of epoxide and ground until the calcite was exposed. The samples were rough polished with 5.0 and 0.3 micron grit size aluminum slurries and given a final polish with a fine aluminum slurry (0.05 grit size) or diamond paste (0.025 grit size). The grinding and polishing steps were the most tedious because of the friability of the calcite relative to the epoxide. Other mounting media considered, such as Canada balsam, are even softer and are thermally less stable under the electron beam.

Most specimens were mounted convex side up so that the polished tangential section of the carapace had a width of at least 15 microns. The area of the carapace eliminated by such sections usually included most of the muscle scars. For several specimens, the carapace was ground differently so that this muscle scar area could be examined to discover whether it differed greatly from the rest of the carapace in magnesium content. For those specimens studied, it apparently did not (Cadot, 1974, Appendix III, table 2).

The polished section of each specimen was then drawn with a camera lucida or photographed. These pictures were used as maps on which each microprobe analytical spot was plotted (Figs. 1 and 2). In this way valves could be examined closely for magnesium zonation within the exposed tangential section.

Prior to analysis, each sample disk was coated with a light carbon shadow of approximately 10 Å thickness. This produced the requisite sample conductivity but did not seriously hamper visibility of the specimen through the optical system

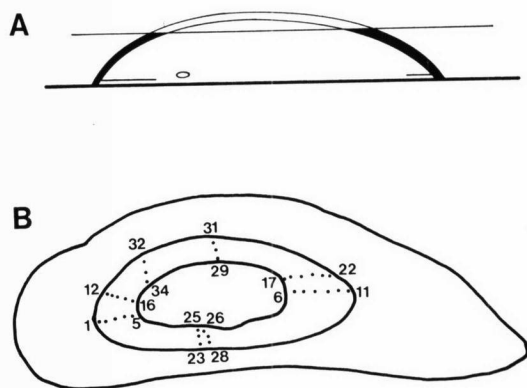


FIG. 1.—A. Diagrammatic polished section of an ostracode valve. The blackened portion remains after sectioning; the unblackened portion is destroyed by polishing—B. A specimen of *Paracypris* showing the relationship of the section to the carapace outline and points of analysis with the electron microprobe analyzer.

of the microprobe. To insure sufficient conductivity between samples and the sample holders, margins of the sample disks were painted with a highly conductive silver compound.

The instruments used were ARL-EMX Microprobe Analyzers at the Smithsonian Institution and the Virginia Polytechnic Institution and State University (see Acknowledgments). The standard used for magnesium was a dolomite standard (USNHM R 10057) containing 20.97 percent MgO, 29.71 percent CaO, 0.66 percent FeO, 0.03

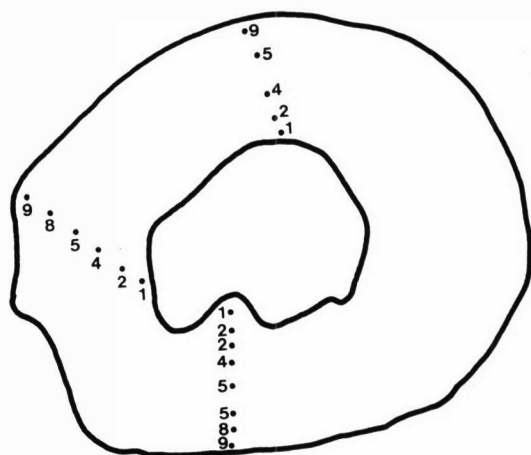


FIG. 2. Outline of the sectioned surface of a specimen of *Loxoconcha* showing typical designations of numbers used to indicate locations within the carapace. [See text for explanations.]

percent MnO, 46.64 percent CO₂, and 0.28 percent HCl insolubles. The standard for calcium was pure Iceland spar in which no magnesium was detected. No attempt was made to correct for magnesium that may have been contained by the interstitial organic material.

DATA PROCESSING

The raw data, ten-second counts of X-ray intensity, were reduced to weight percent CaCO₃ and weight percent MgCO₃ and were corrected for background radiation, mass absorption, atomic number effects, and drift of the beam current and spectrometer. For further details see Cadot (1974, Appendix IV). Aberrant X-ray counts resulted when the calcite was of insufficient thickness, as at the feather edge of a cross section; however, these abnormal counts could be identified and eliminated. Calcium and magnesium were measured simultaneously by using separate spectrometers, so that when calculated as weight percent calcium and magnesium carbonate, the sum should be close to 100 percent. Analyses summing to 100 ± 10 percent were probably acceptable. To reduce the possibility of analytical error, however, only those analyses with sums of 100 ± 5 percent were included in the statistical analysis on which conclusions were based. All analyses used were then normalized so that the calcium and magnesium carbonate summed to 100 percent. Of the some 5,500 analyses, 4,190 or about 75 percent were used in the statistical analysis.

Each analysis, identified by its own number, specimen number, and number within specimen, was converted to mole percent MgCO₃ and entered onto a computer card with a quality design-

ation of satisfactory (summing to 100 ± 5 percent), fair (summing to 100 ± 10 percent), or poor. To cards bearing results of satisfactory or fair analyses, a number was given to indicate the location of the analysis spot within the section (Fig. 2). Location number 1 was assigned to the innermost portion of the carapace section; location number 9 was assigned to the outermost portion, the most distal to the soft parts of the body. In several large specimens of *Macrocypris* there appeared to be a distinct inner layer, and for these individuals the designations were 3, analyses within the inner layer; 6, analyses marginal to the inner layer; and 7, analyses outside the marginal layer. Henceforth locations 1, 2, and 3 will be called the inner region; locations 4, 5, and 6 will be called the middle region; and locations 7, 8, and 9 will be called the outer region.

Finally, to each card was added the water temperature, depth, and latitude from which the specimen was collected plus a number designating the superfamily group and genus to which that specimen belonged. The satisfactory data used in the statistical analysis are presented in this final form in Appendix V of Cadot (1974).

STATISTICAL METHODS

To examine differences in percent MgCO₃ in ostracodes from different environments, collecting localities were pooled into nine station groups, each group containing stations of similar depth and temperature. These station groups are listed with their temperature and depth ranges in Table 3. Satisfactory data from microprobe analyses were then grouped and arranged to test for sig-

TABLE 3. Station Groups Used in Kruskal-Wallis Tests for Significance of Differences in Mean Mole Percent MgCO₃ among Ostracode Superfamily Groups and Carapace Regions.

| Station Group | Stations | Annual Range of Temperature, °C | Range of Depth, m |
|---------------|----------------------|---------------------------------|-------------------|
| I | 11,17 | -1.0- 2.2 | 252-613 |
| II | 2, 6, 8, 10, 32, 34 | 0.9- 2.2 | 2377-4785 |
| III | 4, 33, 35-39 | 2.8- 4.0 | 950-2159 |
| IV | 18, 19, 30, 31 | 4.4- 5.0 | 286-527 |
| V | 26, 29 | 6.1- 6.8 | 1-214 |
| VI | 20, 24, 28 | 6.5- 9.0 | 1-60 |
| VII | 40-42, 51-52, 54, 57 | 12.9-17.0 | 1-2 |
| VIII | 43-46 | 24.8-26.0 | 1-2 |
| IX | 47-49, 55-56, 58 | 27.1-30.0 | 1-33 |

nificant differences in mean mole percent magnesium carbonate at three different levels:

- 1) among the nine station groups;
- 2) among the four superfamily groups within station groups;
- 3) among the three regions of polished section (inner, middle, outer) within each superfamily group and within each station group.

More than 90 percent of the 90 samples at level 3 appeared to be normally distributed after log transformation; however, only three of the nine station groups showed homogeneous variances among means of carapace regions (Cadot, 1974, Appendix VI). Furthermore, although magnesium content, depth, and temperature are all continuously distributed, the temperatures chosen for the study were not normally distributed (Cadot, 1974, Appendix VI). Because product-moment correlation and nested analysis of variance require that variables be normally distributed and that variances at level 3 be homogeneous, it was decided that conclusions should be based on distribution-free statistical analysis using ranked data.

The distribution-free analog of analysis of variance used was the Kruskal-Wallis test, which has an efficiency of 95.5 percent of analysis of variance (Siegel, 1956). The Kruskal-Wallis one-way analysis of variance is designed to determine whether independent samples belong to the same population. It tests "whether the differences among the samples signify genuine population differences or whether they represent merely chance variations such as are to be expected

among several random samples from the same population" (Siegel, 1956, p. 184). Spearman's rank correlation coefficient was used to test for significant correlations. According to Siegel (1956), it is 91 percent as efficient as Pearson's product-moment correlation coefficient. Parametric multiple correlation (with stepwise regression) and nested analysis of variance were also computed, but results of these tests were used only as further evidence supporting results of the distribution-free tests and not as true statistical tests.

Designs to test for significance of differences among means (mole percent MgCO_3) using the Kruskal-Wallis test were as follows:

1) For each station group, individual microprobe analyses were pooled into the four superfamily groups and tested to see if the means among superfamily groups differed significantly.

2) In each superfamily group within each station group, analyses were pooled into inner, middle, and outer carapace regions to see if significant differences existed among the three region means. Pooling of analyses directly into superfamily groups was considered justified and advisable for three reasons. First, it increased sample sizes and hence the power of the statistical tests. Second, the proportion of analyses of inner, middle, and outer carapace regions of satisfactory quality was not constant from specimen to specimen. Third, little difference existed between means of superfamily groups whether calculated from means of specimens or calculated from all analyses (see Table 5).

TABLE 4. *Groups of Data Tested for Correlation between Mole Percent MgCO_3 and Temperature (M-T), between Mole Percent MgCO_3 and Depth (M-D), and between Temperature and Depth (T-D) Using Spearman's Rank Correlation Coefficient (s) and Pearson's Product-moment Correlation Coefficient (r).*

| Groups | Date Tested |
|--|-----------------------|
| a) All Ostracoda (Chave design): | (s) For M-T, M-D, T-D |
| b) Superfamily groups: | (r) For M-T, M-D, T-D |
| c) Carapace region within each superfamily group: | (s) for M-T, M-D |
| d) Locations within carapace regions within superfamily groups: | (r) for M-T, M-D, T-D |
| e) Genera (for those genera present in sufficient numbers): | (s) for M-T |
| f) Some of above genera separated into carapace region within genus: | (r) for M-T, M-D, T-D |
| | (s) for M-T |
| | (r) for M-T, M-D, T-D |
| | (r) for M-T, M-D, T-D |

The groups of data in Table 4 were tested for correlation between mole percent magnesium carbonate and temperature, between mole percent magnesium carbonate and depth, and between temperature and depth using Spearman's rank correlation coefficient (*s*) and Pearson's product-moment correlation coefficient (*r*).

All of the groupings shown in Table 4 yielded sample sizes greater than nine so that the Spearman's rank correlation coefficient (as well as the parametric coefficients) could be tested for significance using the t-test. The cost of computer calculation of parametric correlation coefficients was much less than that of the Spearman's cor-

relation coefficient because the latter required a ranking procedure that was unwieldy and time-consuming. For this reason, results of the parametric tests were obtained first and used to eliminate some designs, deemed unnecessary, from the Spearman testing procedure.

Statistical tests were performed at The University of Kansas Computation Center using the following library programs: Biometry (from Sokal & Rohlf, 1969; modified for larger sample sizes), Biomedical Computer Programs (BMDO2R from the U.C.L.A. Health Science Computing Facility), and Scientific Subroutine Package (SSPOBJ supplied by IBM).

RESULTS AND DISCUSSION

Results of the 4,190 analyses used in the statistical analysis and from which all means were calculated are tabled in Appendix V of Cadot (1974) along with the mean of each specimen. Magnesium carbonate ranges from less than 0.1 to 11.9 mole percent. The mean calculated from all analyses of all ostracode specimens is 3.5 mole percent. The mean mole percents for each of the four superfamily groups are shown in Table 5; cypridaceans have the most magnesium carbonate (5.2 mole percent), and cytheraceans have the least (1.9 mole percent). Means for the inner, middle, and outer regions of the carapace are given with confidence limits for each of the four superfamily groups in Table 6 (see also Fig. 3). The means of each carapace region within each superfamily group are given for the nine station groups in Table 7 and are shown graphically in

Figure 4. Means for the locations within each carapace region are given for the four families in Table 8. Table 9 shows means calculated for selected genera.

MAGNESIUM CONCENTRATION
IN OSTRACODA

According to Blatt, Middleton, and Murray (1972), the ratio of mole percent magnesium to mole percent calcium averages only about 0.05 in calcitic skeletal material compared with 5.20 in sea water. For the ostracodes studied, the average ratio was 0.04 and thus appeared to be consistent with that of other organisms; however, most of the ostracodes studied appeared somewhat unusual in that their calcite had magnesium concentrations designated as intermediate by Milliman (1974), that is, between 1 and 8 mole

TABLE 5. *Ranges and Means of Mole Percent MgCO₃ in Superfamily Groups, Including Means Determined by Averaging Specimen Means within Superfamily Groups and Means Determined by Averaging All Analyses within Superfamily Groups.*

| | Number of Analyses | Superfamily Group Mean | Standard Error | Range of Means of Carapace Regions | Mean of Specimen Means within Superfamily | Range of Specimen Means within Superfamily |
|---------------------|--------------------------|---------------------------|-------------------|--|--|---|
| Platycopina | | | | | | |
| Cytherellidae | 855 | 4.4 | 0.08 | 1.5-8.2 | 4.7 | 1.3-8.4 |
| Podocopina | | | | | | |
| Bairdiacea | 1049 | 4.3 | 0.05 | 1.6-6.4 | 4.3 | 1.4-7.4 |
| Cypridacea | 719 | 5.2 | 0.08 | 3.0-8.5 | 5.5 | 2.8-8.9 |
| Cytheracea | 1567 | 1.9 | 0.04 | 0.1-3.7 | 1.8 | 0.6-5.1 |

TABLE 6. Mean Temperature and Mean and Standard Error of Mole Percent $MgCO_3$ for the Three Regions of Carapace within Each Superfamily Group.

| | Number of Analyses | $MgCO_3$ Mean Mole % | Standard Error | Temperature Mean °C |
|---------------|--------------------------|-------------------------|-------------------|------------------------|
| Platycopina | | | | |
| Cytherellidae | | | | |
| INNER | 214 | 6.22 | 0.133 | 15.3 |
| MIDDLE | 384 | 3.99 | 0.102 | 12.3 |
| OUTER | 257 | 3.41 | 0.114 | 12.2 |
| Podocopina | | | | |
| Bairdiacea | | | | |
| INNER | 292 | 4.92 | 0.097 | 13.3 |
| MIDDLE | 472 | 3.84 | 0.055 | 13.8 |
| OUTER | 285 | 4.43 | 0.114 | 14.0 |
| Cypridacea | | | | |
| INNER | 208 | 6.40 | 0.127 | 10.0 |
| MIDDLE | 235 | 4.87 | 0.124 | 10.1 |
| OUTER | 276 | 4.50 | 0.110 | 8.8 |
| Cytheracea | | | | |
| INNER | 456 | 2.05 | 0.076 | 13.5 |
| MIDDLE | 626 | 1.76 | 0.004 | 14.2 |
| OUTER | 523 | 1.78 | 0.054 | 13.6 |

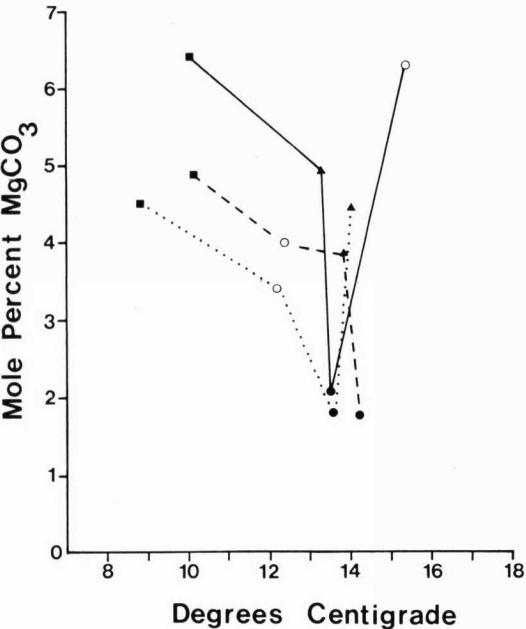


FIG. 3. Mean values of mole percent $MgCO_3$ in inner, middle, and outer regions of the carapace for the four superfamily groups at various temperatures. Open circles indicate Cytherellidae; triangles indicate Bairdiacea; squares indicate Cypridacea; and black circles indicate Cytheracea. Means for inner region connected by solid line; means for middle region connected by dashed line; means for outer region connected by dotted line.

percent. According to Milliman (1974, p. 143), "magnesium concentrations can be high or low but seldom in between. . . . The only organisms that contain intermediate amounts of magnesium are the cephalopod *Argonauta* and some benthonic foraminifera." It would appear that most marine Ostracoda should be added to this list.

A number of workers have suggested that the amount of magnesium substituted in calcitic skeletons is largely a function of phylogeny and that there has been a biochemical evolution in the ability of organisms to discriminate against the magnesium ion during shell construction (Chave, 1954; Dodd, 1967; Blatt, Middleton, & Murray, 1972; Milliman, 1974). Results of our study appear to support this conclusion in that the cytheraceans, the superfamily generally considered to be the most highly evolved marine ostracode group, contains considerably less magnesium than the other three superfamilies, but this result may be complicated by magnesium associated with interstitial organic material rather than calcite of the carapace. Whereas the cytheraceans did not evolve until the late Paleozoic, but dominate post-Paleozoic marine faunas, the bairdiaceans, cypridaceans, and cytherellaceans have lineages extending far back into the Paleozoic.

The origin of these superfamilies is not well

TABLE 7. Mean Mole Percent $MgCO_3$ of Carpace Regions within Superfamily Groups for Each Station Group and Results of Kruskal-Wallis Tests Including H-statistics and Levels of Significance. [Explanation: NS, not significant, $P > 0.05$; *, significant at $P < 0.025$; †, significant at $P < 0.01$; ‡, significant at $P < 0.005$; §, too many tied variates for analysis.]

| Station Group | Superfamily Group | Carapace Region Means Inner/Mid/Outer | H-statistic Among Regions | H-statistic Among Families |
|---------------|-------------------|---------------------------------------|---------------------------|----------------------------|
| 1 | Cypridacea | 5.13/3.70/3.56 | 27.8‡ | 27.6‡ |
| | Cytheracea | 0.22/0.14/0.14 | 4.5 NS | |
| 2 | Cytherellidae | 4.18/2.60/2.19 | 10.2‡ | 500.1‡ |
| | Bairdiacea | 2.49/1.65/1.64 | 26.5‡ | |
| | Cypridacea | 6.01/3.29/2.96 | 97.7‡ | |
| | Cytheracea | 0.91/0.72/0.59 | 27.5‡ | |
| 3 | Cytherellidae | 4.31/1.87/1.53 | 19.7‡ | 275.7‡ |
| | Bairdiacea | 3.78/2.95/2.38 | 26.1‡ | |
| | Cypridacea | 6.10/5.89/4.90 | 5.5 NS | |
| | Cytheracea | 1.51/0.91/0.74 | 13.1‡ | |
| 4 | Bairdiacea | 5.35/4.53/4.12 | 19.9‡ | 87.7‡ |
| | Cypridacea | 6.45/5.83/5.62 | 7.6* | |
| | Cytheracea | 1.16/1.41/1.76 | 1.2 NS | |
| 5 | Cypridacea | 4.49/4.96/4.37 | 2.0 NS | 82.8‡ |
| | Cytheracea | 1.76/1.31/1.27 | 14.4‡ | |
| 6 | Cytherellidae | 4.57/2.83/2.03 | 101.0‡ | 58.4‡ |
| | Bairdiacea | 4.51/3.43/3.47 | 47.0‡ | |
| | Cytheracea | 3.68/1.50/1.09 | 19.7‡ | |
| 7 | Cytherellidae | 6.58/5.56/5.12 | 44.1 | 109.9‡ |
| | Bairdiacea | 5.26/3.95/4.47 | 36.9 | |
| | Cypridacea | 5.80/4.72/5.13 | 17.5 | |
| | Cytheracea | 1.56/1.63/1.91 | § | |
| 8 | Cytherellidae | 6.55/5.29/4.69 | 13.5‡ | 407.2‡ |
| | Bairdiacea | 5.99/4.63/6.41 | 121.2‡ | |
| | Cypridacea | 8.37/7.24/6.84 | 30.4‡ | |
| | Cytheracea | 3.62/2.84/2.98 | 13.1‡ | |
| 9 | Cytherellidae | 8.24/5.85/4.45 | 82.7‡ | 270.6‡ |
| | Bairdiacea | 5.63/4.32/5.16 | 13.9‡ | |
| | Cypridacea | 8.52/6.75/7.91 | 10.5‡ | |
| | Cytheracea | 3.33/2.85/3.04 | 2.4 NS | |

understood, but bairdiaceans are known from the Ordovician onward and are commonly known to be conservative in morphological characters (Bolz, 1971). Cypridaceans may have evolved from bairdiaceans in early Paleozoic time (Moore, 1961); however, Maddocks (1972) suggested that the cypridaceans as well as the bairdiaceans might be closely related to saipanettid healdiaceans of Suborder Metacopina. Maddocks believed cytheraceans to be more distantly related but that all three superfamilies may have "healdiacean ancestry with saipanettid internal anatomy"

(Maddocks, 1972, p. 30). The Suborder Platycopina including Cytherellidae, was thought to be much more distantly related to the other groups (Maddocks, 1972). Adamczak (1971) actually included the genus *Cytherella* within the Order Paleocopida. If he was correct, the Cytherellidae and possibly a few species of Punciidae are the only living representatives of the Paleocopida. According to Adamczak and also Loranger (1971), the genus *Cytherella* was an important constituent of Middle Devonian faunas.

According to Chave's results, the Ostracoda

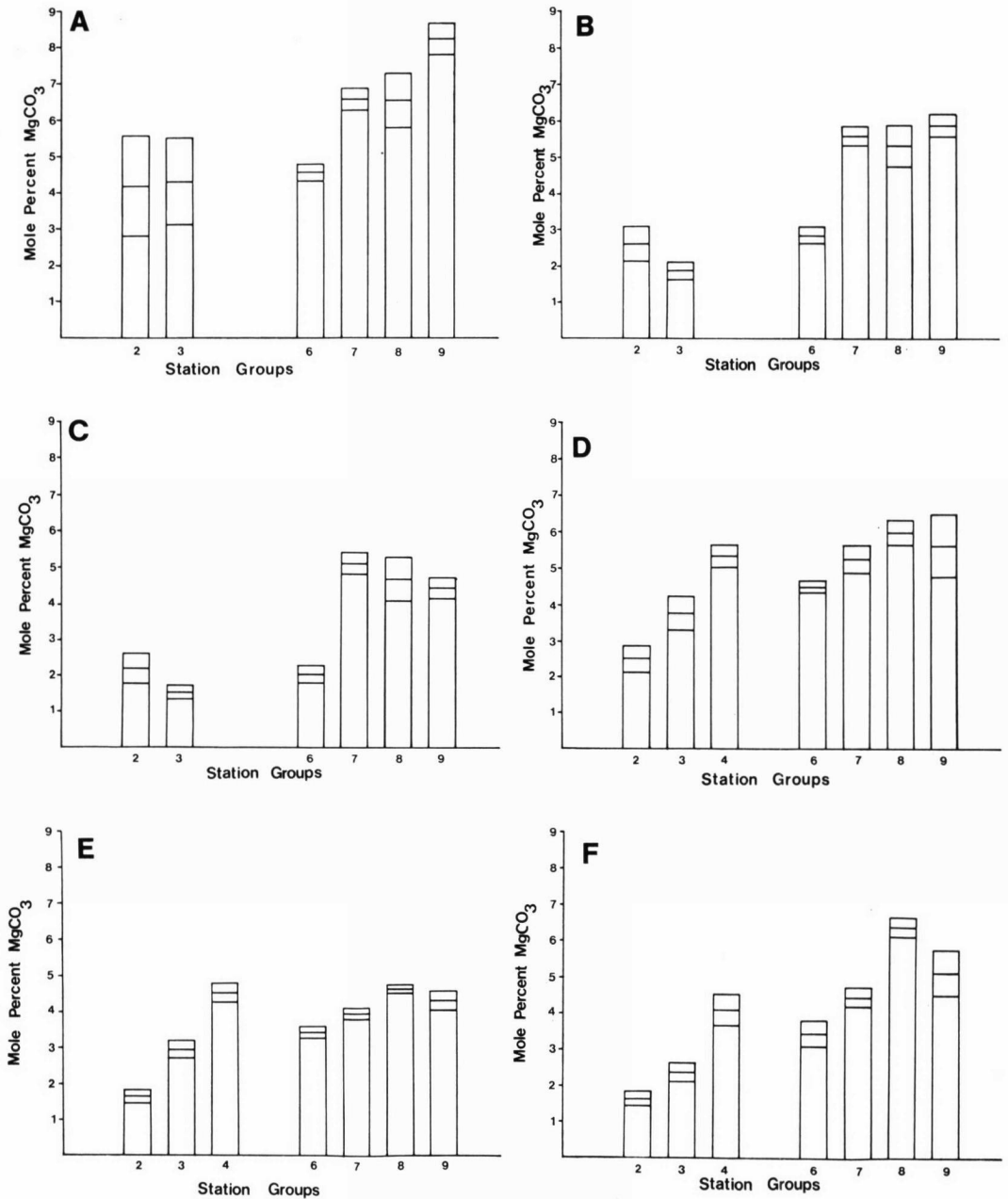


FIG. 4.—A. Bar graph showing mean and 95-percent confidence limits of the concentration of MgCO_3 in mole percent for the inner carapace region of specimens of Cytherellidae from each of the nine stations from which specimens were analyzed.—B. Middle carapace region of Cytherellidae.—C. Outer carapace region of Cytherellidae.—D. Inner carapace region of Bairdiacea.—E. Middle carapace region of Bairdiacea.—F. Outer carapace region of Bairdiacea.—G. Inner carapace region of Cypridacea.—H. Middle carapace region of Cypridacea.—I. Outer carapace region of Cypridacea.—J. Inner carapace region of Cytheracea.—K. Middle carapace region of Cytheracea.—L. Outer carapace region of Cytheracea.

as a class have too much magnesium substitution for their phyletic level (Chave, 1954; Dodd, 1967); however, results of our study suggest that magnesium incorporation averages less than Chave's results indicated. In the cytheraceans

studied, magnesium carbonate averages just under 2 mole percent, and according to Plummer and McKenzie (1972), the most stable form of calcite (at 25° C) is that containing 2 mole percent magnesium carbonate. It should also be noted

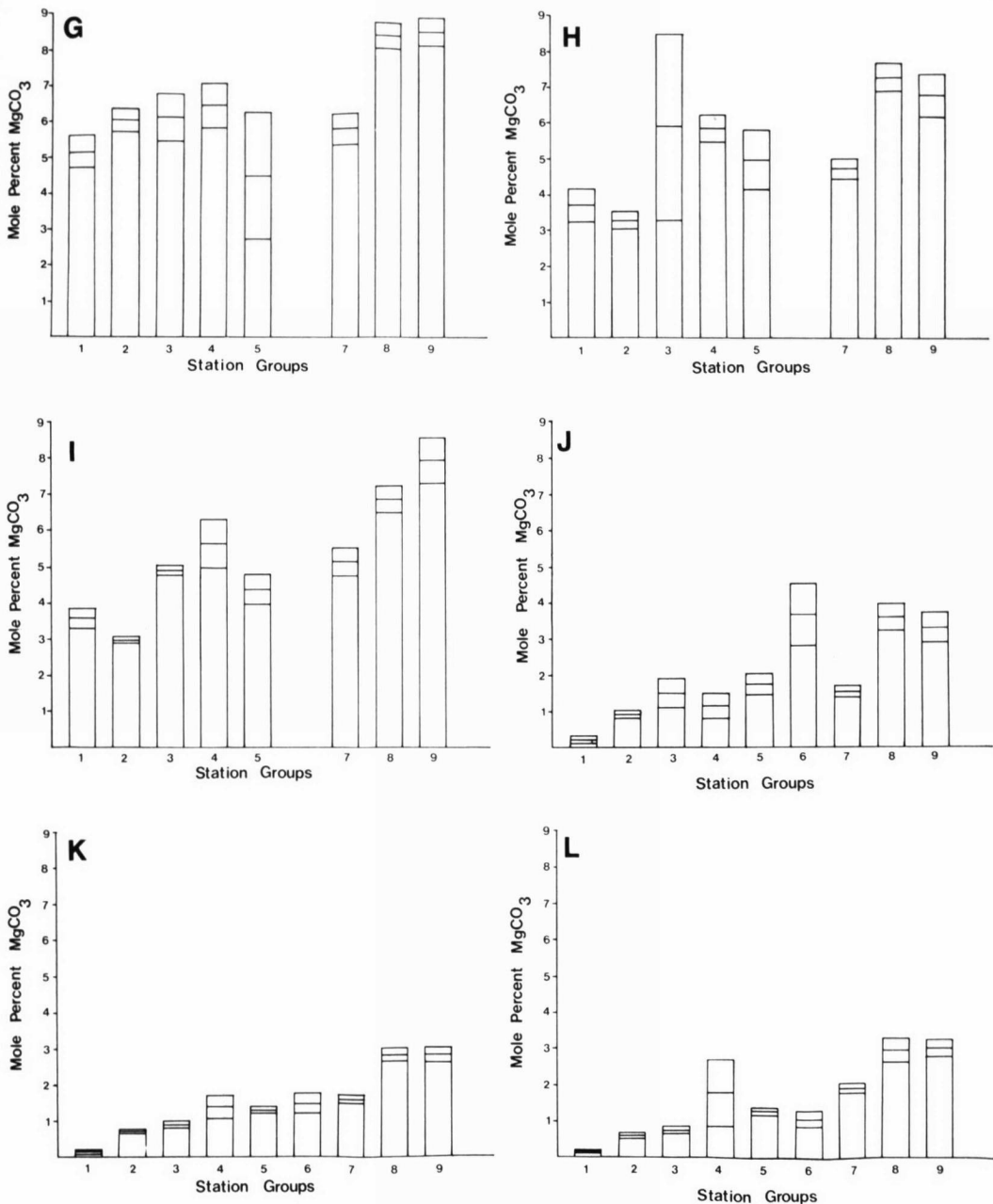


FIG. 4. (Continued from facing page.)

TABLE 8. Mean Temperature and Mean Mole Percent $MgCO_3$ with Standard Error for Locations within Carapace Regions within Superfamily Groups.

| | Carapace Location | Number of Analyses | $MgCO_3$ Mean Mole % | Standard Error | Temperature Mean °C |
|---------------|-------------------|--------------------|----------------------|----------------|---------------------|
| Cytherellidae | 1 | 123 | 6.92 | 0.065 | 16.9 |
| | 2 | 91 | 5.26 | 0.174 | 13.0 |
| | 4 | 167 | 4.46 | 0.143 | 13.4 |
| | 5 | 217 | 3.63 | 0.139 | 11.4 |
| | 8 | 117 | 3.38 | 0.174 | 10.3 |
| | 9 | 140 | 3.42 | 0.152 | 13.7 |
| Bairdiacea | 1 | 181 | 5.17 | 0.134 | 13.1 |
| | 2 | 112 | 4.52 | 0.126 | 13.8 |
| | 4 | 212 | 3.93 | 0.078 | 14.4 |
| | 5 | 250 | 3.75 | 0.077 | 12.9 |
| | 8 | 138 | 4.09 | 0.128 | 14.1 |
| | 9 | 147 | 4.76 | 0.182 | 13.8 |
| Cypridacea | 1 | 76 | 6.97 | 0.229 | 13.3 |
| | 2 | 65 | 6.33 | 0.234 | 15.1 |
| | 3 | 67 | 5.81 | 0.107 | 1.5 |
| | 4 | 74 | 5.43 | 0.229 | 13.7 |
| | 5 | 94 | 5.42 | 0.185 | 13.8 |
| | 6 | 67 | 3.49 | 0.137 | 1.3 |
| | 7 | 110 | 3.20 | 0.068 | 1.5 |
| | 8 | 70 | 5.17 | 0.223 | 13.5 |
| | 9 | 96 | 5.48 | 0.187 | 13.7 |
| Cytheracea | 1 | 250 | 2.20 | 0.109 | 14.0 |
| | 2 | 206 | 1.86 | 0.092 | 12.1 |
| | 4 | 250 | 1.82 | 0.069 | 15.4 |
| | 5 | 338 | 1.67 | 0.058 | 13.6 |
| | 8 | 225 | 1.63 | 0.074 | 13.0 |
| | 9 | 298 | 1.89 | 0.077 | 14.1 |

TABLE 9. Mean Temperature and Mean Mole Percent $MgCO_3$ with Standard Deviation for Selected Genera within Superfamily Groups (selected genera with sample size greater than 60).

| | Number of Analyses | $MgCO_3$ Mean Mole % | Standard Deviation | Temperature Mean °C |
|--|--------------------|----------------------|--------------------|---------------------|
| I Cytherellidae | | | | |
| <i>Cytherelloidea</i> | 711 | 4.86 | 2.05 | 15.5 |
| <i>Cytherella</i> | 182 | 2.19 | 1.33 | 3.3 |
| II Bairdiacea | | | | |
| <i>Bairdia</i> | 891 | 4.62 | 1.46 | 15.5 |
| <i>Bythocypris</i> | 143 | 2.25 | 0.79 | 2.0 |
| III Cypridacea | | | | |
| <i>Paracypris</i> | 184 | 6.45 | 1.79 | 20.8 |
| <i>Propontocypris</i> | 88 | 7.00 | 2.55 | 21.9 |
| <i>Argilloecia</i> | 76 | 5.74 | 1.06 | 5.3 |
| <i>Macrocypris</i> | 357 | 3.96 | 1.50 | 1.1 |
| IV Cytheracea | | | | |
| <i>Henryhowella</i> | 132 | 0.61 | 0.42 | 2.7 |
| <i>Bradleya</i> | 64 | 1.10 | 0.67 | 3.7 |
| <i>Krithe</i> | 213 | 1.00 | 0.35 | 3.6 |
| <i>Xestoleberis</i> | 210 | 2.01 | 1.32 | 13.4 |
| <i>Haplocytheridea</i> | 176 | 2.73 | 0.79 | 26.1 |
| <i>Loxoconchidae</i> | 249 | 3.11 | 1.19 | 20.5 |
| (<i>Loxoconcha</i> , <i>Loxocorniculum</i> , ? <i>Loxoconchella</i>) | | | | |

again that because ostracodes grow by molting, calcification takes place very rapidly, perhaps reducing the ability of members of the class to discriminate against magnesium. During periods of rapid calcification, some aquipecten bivalves also incorporate higher amounts of magnesium (Moberly, 1968).

TESTS OF HYPOTHESES

PHYLOGENETIC CONTROL OF MAGNESIUM

Milliman (1974), using foraminifers, corals, and bryozoans as examples, concluded that mineralogy can vary among classes within phyla and among orders within classes, as well as among phyla. For ostracodes it was hypothesized earlier that significant variation may take place among superfamilies. Results of the Kruskal-Wallis test, shown in Table 7, support this hypothesis. Differences among the superfamily groups were highly significant within the nine station groups (H-statistics significant at $P < 0.005$).

It is interesting to note that results of the nested analysis of variance test supported those of the Kruskal-Wallis test. These results (Cadot, 1974, Appendix II) suggested that there were highly significant differences among the four superfamily groups and also among the three carapace regions. The nested analysis of variance also tested for significant difference among all microprobe analyses, a design which could not be used for the Kruskal-Wallis test because of the large sample size. By pooling all analyses regardless of superfamily group, Chave's (1954) samples were approximated (ostracodes mixed without regard for taxonomic affiliation). Results of the nested analysis of variance suggested that at this level, which disregarded superfamily membership, differences in magnesium content due to temperature were not significant. Results of the Kruskal-Wallis test, however, showed that when differences among superfamily groups were considered, differences in magnesium content were highly significant even though specimens were drawn from environments with similar temperatures.

VARIATION WITHIN CARAPACES

Weber (1973) reported consistent differences among parts of individual echinoids, especially coronal plates versus spines. Milliman (1974)

summarized most other recent studies of biogenic calcite including the microprobe work of Moberly (1968) and Cadot, Van Schmus, and Kaesler (1972). At the end of his summary, Milliman (1974, p. 147) concluded that "even in organisms with constant mineralogy [i.e., all calcite or all aragonite] . . . elemental concentrations may change within different layers."

Results of the Kruskal-Wallis test applied to our data indicated that for the Cytherellidae and the Bairdiacea, differences in mole percent magnesium carbonate among inner, middle, and outer regions of sections across the carapace were highly significant ($P < 0.005$), even when the samples included were restricted to a single station group (Table 7; Fig. 4, *D-F*). Cypridaceans also showed significant differences among regions, but not at all station groups ($P < 0.025$ for 6 of 8 groups; Table 7; Fig. 4, *G-I*). Cytheraceans showed significant variation ($P < 0.01$) within only 4 of 8 station groups. A ninth station group, number 7, contained too many tied variates for the computer program used. Because the cytheraceans are thought to be more highly evolved, they might be expected to show a more uniform distribution of magnesium within their carapaces (Figs. 4, *K*, and 4, *L*). MacQueen, Ghent, and Davies (1974) observed from their microprobe study of three specimens of sand dollars and from other studies of echinoids by Weber (1969) and Schroeder (1969) that heterogeneous distributions of magnesium in echinoderm skeletons is fairly common. They then cited Cadot, Van Schmus, and Kaesler (1972) and concluded that variation in magnesium carbonate content may be common in skeletal calcite from a variety of phyla. "Such inhomogeneities in magnesium carbonate add another variable to the relationship between magnesium carbonate on the one hand, and water temperature and phylogenetic level on the other" (MacQueen, Ghent, & Davies, 1974, p. 67).

CORRELATION OF MAGNESIUM CONTENT WITH WATER TEMPERATURE

Spearman's rank correlation coefficients and results of t-tests for significance are given in Tables 10 to 12. Parametric correlation coefficients were not calculated.

The results indicate that much of the variation shown above to be significant is correlated with temperature. Temperature is known to be cor-

TABLE 10. *Spearman's Rank Correlation of $MgCO_3$ Content with Temperature and Depth; All Coefficients Significant at $P < 0.001$.*

| | Correlation of $MgCO_3$ Content: | |
|--|----------------------------------|------------|
| | with temperature | with depth |
| Cytherellidae (all regions) | 0.69 | -0.72 |
| Inner region | 0.71 | -0.67 |
| Middle region | 0.74 | -0.76 |
| Outer region | 0.71 | -0.77 |
| Bairdiacea (all regions) | 0.60 | -0.57 |
| Inner region | 0.53 | -0.51 |
| Middle region | 0.57 | -0.53 |
| Outer region | 0.78 | -0.73 |
| Cypridacea (all regions) | 0.66 | -0.56 |
| Inner region | 0.56 | -0.35 |
| Middle region | 0.72 | -0.61 |
| Outer region | 0.82 | -0.75 |
| Cytheracea (all regions) | 0.78 | -0.72 |
| Inner region | 0.69 | -0.52 |
| Middle region | 0.82 | -0.62 |
| Outer region | 0.82 | -0.63 |
| Ostracoda (containing all superfamily groups and all carapace regions) | | |
| Sample 1 | 0.41 | -0.41 |
| Sample 2 | 0.46 | -0.45 |
| Sample 3 | 0.40 | -0.40 |

related with depth but also with latitude. It should be remembered that ostracode growth rate is not an important factor in explaining correlation between temperature and magnesium concentration. Rapid calcification, instantaneous relative to most other groups, is requisite for survival of the individual and therefore may explain the presence of magnesium in Ostracoda but seems unlikely to be a source of significant variation among taxonomic groups within the class.

To test further Chave's (1954) design, all analyses were pooled into one of three samples, each containing analyses from all three carapace regions and each with approximately a third of the analyses within each of the four superfamily groups. Ideally, all analyses should have been pooled into a single sample, but this was not done because of the expense of ranking such a large sample. Spearman's rank correlations of magnesium concentration with temperature and with depth were low but significant (Table 10). On the other hand, correlations of temperature with depth were high, about -0.8. The large amount of scatter caused by disregarding taxonomy was graphically demonstrated when means of specimens from all four families were plotted on the same temperature-magnesium scatter diagram (Fig. 5, A). A fortuitous selection of specimens could, in spite of disparate superfamily affiliation, produce the good correlation found by Chave (see Fig. 5, F).

The validity of the assumption that a well-defined relationship exists between skeletal magnesium content within a class and water temperature has recently been challenged by Weber (1973), based on his work with echinoderms. At the class level, his data supported his conclusion, but at the order and family level his results were less conclusive. When the Ostracoda studied were separated into superfamily groups, the rank correlation of magnesium content averaged 0.26 higher with temperature and 0.21 higher with depth than when superfamily groups were lumped (Table 10). All coefficients were highly significant ($P < 0.001$). This improvement of correla-

TABLE 11. *Spearman's Rank Correlation of $MgCO_3$ Content in Carapace Location (within Region) with Temperature; All Coefficients Significant at $P < 0.001$ Except the Two Indicated as NS, Not Significant, with $P > 0.05$.*

| Locations: | Inner | | | Middle | | | Outer | |
|---------------|-------|------|----------|--------|------|---------|-------|------|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| Cytherellidae | 0.75 | 0.65 | | 0.72 | 0.77 | | | 0.73 |
| Bairdiacea | 0.59 | 0.48 | | 0.55 | 0.60 | | | 0.74 |
| Cypridacea | 0.76 | 0.73 | -0.16 NS | 0.67 | 0.62 | 0.15 NS | 0.56 | 0.79 |
| Cytheracea | 0.73 | 0.65 | | 0.81 | 0.84 | | | 0.83 |

FIG. 5.—A. Mean mole percent $MgCO_3$ of all specimens regardless of superfamily versus temperature. Open circles indicate depths of 0 to 50 meters; solid circles indicate depths of 200 to 650 meters; solid squares indicate depths of 950 to 4800 meters.—B. Mean mole percent $MgCO_3$ of specimens of Cytherellidae.—C. Mean mole percent $MgCO_3$ of specimens of Bairdiacea.—D. Mean mole percent $MgCO_3$ of specimens of Cypridacea.—E. Mean mole percent $MgCO_3$ of specimens of Cytheracea.—F. Mean mole percent $MgCO_3$ of selected genera versus temperature; all super-

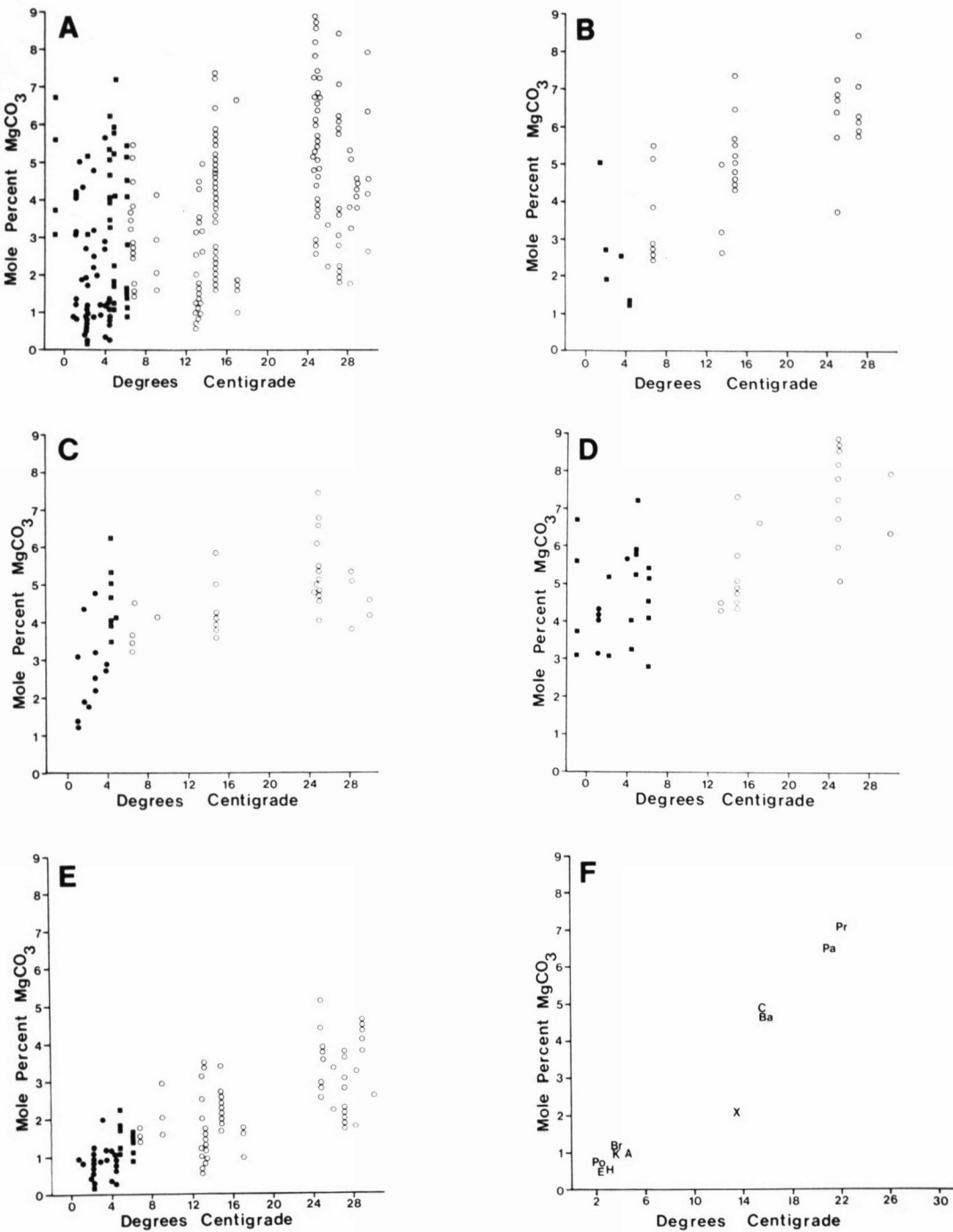


FIG. 5 (Explanation continued from facing page.)

family groups are represented. [Explanation: Cytherellidae: *Cytherella*, C; Bairdiacea: *Bairdia*, Ba; Cypridacea: *Protonocypris*, Pr; *Paracypris*, Pa; Cytheracea: *Krithe*, K; *Xestoleberis*, X; *Henryhowella*, H; unnamed genus A, A; *Poseidonamicus*, Po; *Echinocythereis*, E; *Bradleya*, Br.]

tion of magnesium with temperature was demonstrated graphically by plotting means of specimens first all together and then one superfamily group at a time (Fig. 5, A-E).

On the whole, rank-correlation of magnesium content with temperature was not improved by separating superfamily groups into genera (Tables 12 and 13). The mean for Spearman's rank

TABLE 12. *Spearman's Rank Correlations of MgCO₃ Content with Temperature for Selected Genera; All Correlations Significant at P < 0.001.*

| | Correlation |
|-----------------------|-------------|
| Cytherellidae | |
| <i>Cytherelloidea</i> | 0.61 |
| Bairdiacea | |
| <i>Bairdia</i> | 0.41 |
| <i>Bythocypris</i> | 0.58 |
| Cypridacea | |
| <i>Paracypris</i> | 0.77 |
| <i>Propontocypris</i> | 0.60 |
| Cytheracea | |
| <i>Krithe</i> | 0.60 |
| <i>Bradleya</i> | 0.71 |
| <i>Xestoleberis</i> | 0.41 |
| Loxoconchidae | 0.75 |
| (3 genera) | |

correlations of magnesium content with temperature was 0.60 when genera were considered separately; whereas when genera were pooled into superfamily groups, the mean was 0.68. Only the genus *Paracypris* yielded a higher correlation of magnesium with temperature than its superfamily group as a whole, and this could be the result of small sample sizes. Weber (1973) also noted relatively poor correlation of magnesium with water temperature at the generic level in echinoids even when examination was restricted to a particular part of the skeletons. For instance, for family Echinometridae, Weber reported correlations ranging from 0.26 for *Echinometra* pyramids to 0.66 for *Heterocentrotus* teeth. This is also consistent with the findings of Ponder and Glendenning (1974) for genera of Foraminiferida within the superfamily Miliolacea. Although

TABLE 13. *Means of Spearman's Rank Correlations of MgCO₃ with Temperature for Five Arrangements of Data.*

| Group | Correlation | Mean |
|---|-------------|------------------------|
| Ostracoda: | | |
| Samples of mixed super-families and carapace regions | 0.42 | of 3 |
| Ostracodes separated by superfamily group | 0.68 | of 4 |
| Ostracodes separated into genera within superfamily group | 0.60 | of 9 |
| Ostracodes separated into carapace region within superfamily group | 0.71 | of 4 superfamily means |
| Ostracodes separated into location within region within superfamily group | 0.66 | of 4 superfamily means |

specimens they studied were all collected from localities with similar water temperatures, they found (p. 32) the percent of magnesium carbonate in specimens "of close or distant phyletic affinity is approximately the same." In other words, examination of individual genera within the superfamily Miliolacea did not yield information not gained by studying the superfamily as a whole. Figure 6, A, suggests, however, that the scatter in temperature versus magnesium plots might be decreased by selecting families within superfamilies.

The highest average correlation of magnesium concentration with temperature was obtained by dividing the superfamily groups into carapace regions within superfamily groups (Tables 10 and 13). By averaging Spearman's rank correlation coefficients obtained for the three regions in each superfamily group, the mean correlation of magnesium concentration with temperature was found to be 0.72 for the Cytherellidae, 0.63 for the Bairdiacea, 0.70 for the Cypridacea, and 0.78 for the Cytheracea. The grand mean for the four superfamily groups was 0.71 compared with a mean of 0.68 obtained for the design in which

FIG. 6.—A. Mean mole percent MgCO₃ versus temperature for *Krithe* (family Krithidae), solid circles, and three genera of Loxoconchidae (solid squares).—B. Mean mole percent MgCO₃ of all four superfamily groups versus temperature of the station groups. Where a station group represented more than one water temperature, the mean mole percent MgCO₃ was plotted at both ends of the station group's temperature range, thus producing a horizontal line segment. [Explanation: Cytherellidae, solid squares; Bairdiacea, solid circles; Cypridacea, open circles; Cytheracea, solid triangles.]—C. Mean mole percent MgCO₃ of Cytherellidae versus temperature of the station groups at which they were found. Inner region of carapace, solid triangles; middle region of carapace, solid circles; outer region of carapace,

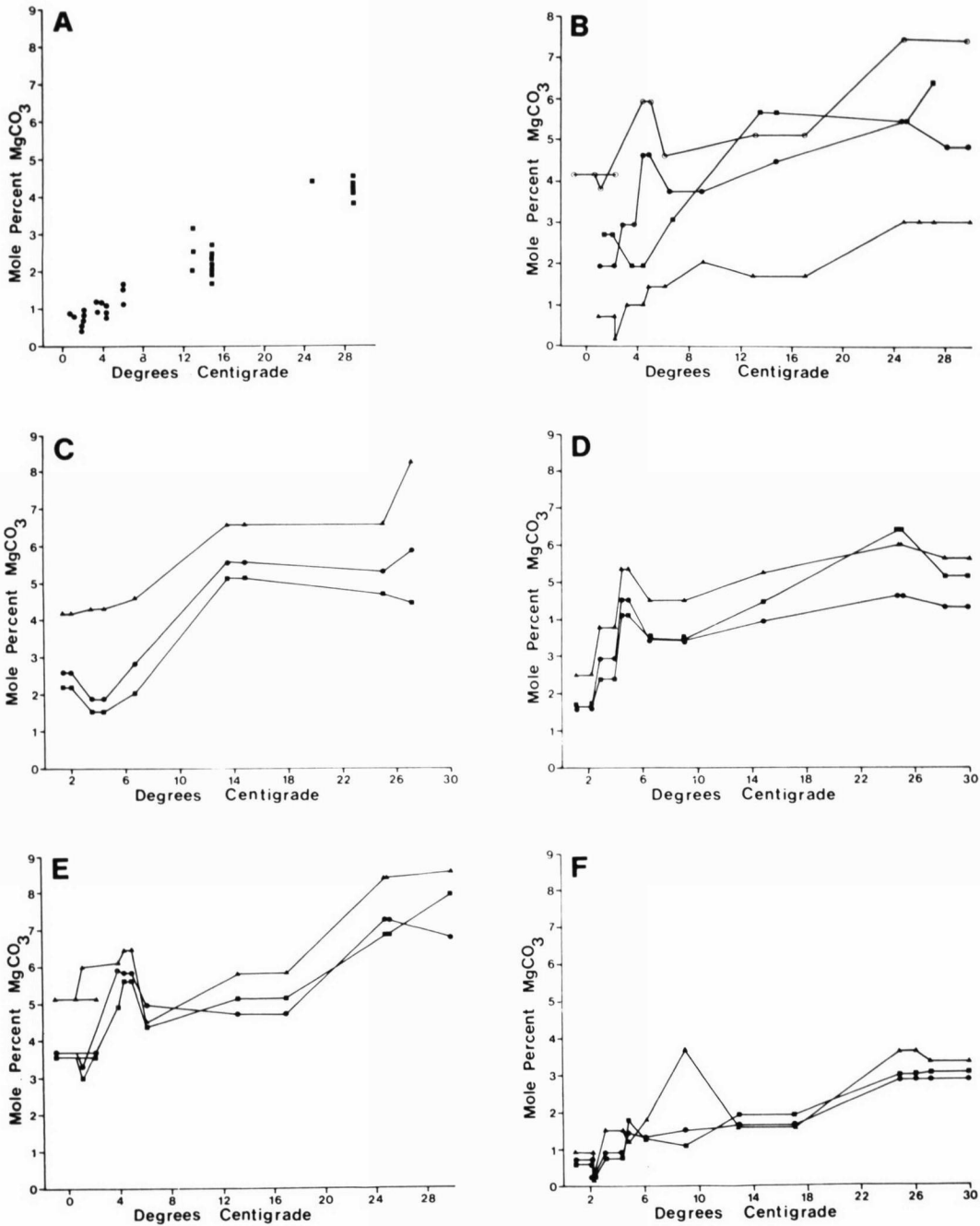


FIG. 6. (Explanation continued from facing page.)

solid squares.—D. Mean mole percent MgCO_3 of Bairdiacea versus temperature of the station groups at which they were found. Symbols are the same as for C.—E. Mean mole percent MgCO_3 of Cypridacea versus temperature of the station groups at which they were found. Symbols are the same as for C.—F. Mean mole percent MgCO_3 of Cytheracea versus temperature of the station groups at which they were found. Symbols are the same as for C.

regions of the carapace were pooled within superfamily groups. On the other hand, the grand mean for correlation of magnesium concentration with depth was only 0.62 compared with 0.61 for the design in which regions of the carapace were pooled. All rank coefficients (magnesium with temperature and with depth) were highly significant at $P < 0.001$ in both designs. The only superfamily group that did not show an increase in magnesium correlation with temperature by division into carapace region was the Cytheracea; however, the Cytheracea yielded the highest correlations of magnesium with temperature in both designs. This may well be a reflection of more uniform magnesium distribution within cytheracean carapaces such that the relationship between temperature and magnesium in the carapace is not as masked by variations within the carapace. This uniformity in cytheraceans relative to other superfamily groups was probably not due to sampling bias because samples of Cytheracea contained the largest number of analyses, specimens, and genera.

The increase of the correlation of magnesium concentration with temperature by separating analyses first into superfamily groups and then into carapace region within superfamily group can be seen graphically in Figures 6,B-F; however, Figure 3 shows that phylogenetic control at the superfamily level is a much more important factor than variation within the carapace in the search for correlation of temperature with concentration of magnesium in Ostracoda.

IMPORTANCE OF TEMPERATURE VERSUS CALCIFICATION RATE

For all four superfamily groups, the magnesium concentration in the inner region of the carapace showed the weakest correlation both with temperature and with depth. Although rate of calcification was probably not a significant factor in differences among superfamily groups or station groups or even among individuals, it could possibly have explained the lower correlation coefficients for the inner region of the carapace. From Tables 6 and 7 and Figures 6,C-F, it can be seen that although the inner region was the least correlated with temperature, it generally contained the highest concentrations of magnesium. Because ostracodes are most vulnerable just after molting, it would seem logical that the

region immediately adjacent to the soft anatomy might be calcified faster, thus causing more magnesium to be incorporated regardless of the temperature of the environment; however, the sequence of events during calcification of Ostracoda is not well understood and needs further study (but see Passano, 1960).

Weber (1973, p. 550) in his study of calcite of echinoids concluded that "a relationship between water temperature and skeletal magnesium is real, but poorly defined . . . and may in fact reflect temperature control of calcification rate rather than a direct temperature-dependent effect in the thermodynamic sense." Davies, Crenshaw, and Heatfield (1972, p. 882), in another study of echinoids, concluded that "the genetic factor is the significant factor, coupled with developmental stage, in controlling chemistry; temperature merely affects rate of growth." Results of our study suggest that for Ostracoda the first part of the statement may be correct, but that temperature is a significant source of variation of magnesium content independent of growth rate. Dodd (1967, p. 1324) wrote that "the temptation to explain temperature effect as resulting from growth rate differences is strong," and Weber (1973, p. 555) concluded that results of his study "do nothing to reduce that temptation"; however, the results of our study may reduce the temptation at least for the ostracodes studied. Calcification rate, rapid for all ostracodes, may, however, explain the base-level of magnesium content about which variation took place.

IMPORTANCE OF LOCATION WITHIN CARAPACE REGION

Tables 11 and 13 show that rank correlations of magnesium content with water temperature tended not to be increased when the three regions of the carapace were divided into the two or three locations per region. This design did not add much information about any superfamily group, with the exception of the cypridaceans, and resulted in smaller sample sizes. Cypridacean locations 3 and 6 (Table 8) represent analyses within and bordering an apparent layer of high magnesium calcite detected only in larger specimens of deep-sea *Macrocypris*, the largest specimens studied. This inner layer, containing about 6 mole percent magnesium carbonate in spite of the cold deep-sea temperature, was not apparent in other

specimens either because it did not exist or because it was too narrow to be detected with the size of electron beam employed. Unfortunately, only a few large *Macrocypris* were collected with soft parts, and those without soft parts were thought to yield unreliable results (Cadot, 1974). Two of the specimens with soft parts were large enough to be sectioned longitudinally, resulting in a truer view of the layer's thickness. It should be noted that if location 3 is removed from the study of the cypridacean inner region as a whole, the correlation found between magnesium of the inner region and temperature is raised to 0.72, a potentially fruitful area of future research.

DEPTH AS AN INDEPENDENT SOURCE OF VARIATION

The contention that depth does not influence magnesium substitution other than by exerting partial control of temperature is difficult to test but is supported by the following evidence:

1) Except when all ostracodes were pooled regardless of taxonomy (Chave's 1954 design), the correlation of magnesium concentration with temperature was greater than with depth except

in the middle and outer carapace region of the Cytherellidae. The reasons for the exception are not known but could be related to the fact that the Cytherellidae belong to a separate suborder and perhaps a separate order from the other ostracodes studied (Bolz, 1971; Adamczak, 1971; Maddocks, 1972).

2) Temperature of the localities studied is not perfectly correlated with depth (Spearman's $\rho = -0.82$) and is also associated with latitude (parametric $r = -0.42$).

3) Results of the parametric multiple correlation with stepwise regression, used as rough indicators, showed that depth was not an important factor in magnesium control (Cadot, 1974, Appendix II). When ostracodes as a whole were tested, temperature was selected as the most important variable. Depth was selected fourth behind latitude and location on carapace in importance when data were separated into the four superfamilies; temperature was again selected as the most important factor in magnesium control. Depth was ranked fourth for Cytheracea and Cytherellidae and was ranked second and third for the Bairdiacea and Cypridacea, respectively.

CONCLUSIONS

1) Magnesium content varied significantly among representatives of ostracode superfamily groups from the same environment. Therefore, the hypothesis that phylogenetic control of magnesium content extends at least to the superfamily level was accepted; however, phylogenetic control at the suborder level was not apparent because analyses of the Cytherellidae (Platycopina) yielded magnesium contents similar to two of the three superfamilies of suborder Podocopina.

2) Magnesium content differed significantly among inner, middle, and outer regions of the carapace sections. Therefore, position within individual carapaces was a significant source of difference in concentration of magnesium carbonate.

3) The hypothesized close correlation between percent magnesium and water temperature was not found at the class Ostracoda level ($r = 0.4$); however, when the data were divided according to superfamily, higher coefficients were obtained

($r = 0.7$) indicating that water temperature was an important source of variation of magnesium concentration in spite of the uniformly rapid calcification rate in Ostracoda. Growth rate, or more properly, calcification rate, may have set the limits for incorporation of magnesium at the class level and may also have been responsible for differences among regions of the carapace within individuals; however, our results indicated that temperature was a significant source of variation within superfamily groups, even though variation of temperature has little effect on the calcification rate of ostracodes.

4) Whereas division of data into superfamily groups and regions of the carapace substantially improved the correlation of magnesium content with temperature, and whereas temperature was associated with latitude as well as depth, it is suggested that depth does not represent a separate source of variation independent of temperature.

Furthermore, although used only as a rough indicator because assumptions of the method were not met by the data, parametric stepwise regression selected temperature as the most important

source of variation for all four superfamilies, whereas depth was found to be less important than temperature, latitude, and location on carapace when all data were considered together.

REFERENCES

- Adamczak, Franciszek, 1971, *On some ostracod assemblages of Middle Devonian rocks*: Paleocologie des Ostracodes, H. J. Oertli (ed.), Centre Rech. Pau, Bull. v. 5 (suppl.), p. 787-800, Société Nationale des Pétroles d'Aquitaine (Pau).
- Bathurst, R. G. C., 1971, *Carbonate sediments and their diagenesis*: Developments in sedimentology 12, 620 p., Elsevier Publ. Co. (Amsterdam).
- Blatt, Harvey, Middleton, G. V., & Murray, R. C., 1972, *Origin of sedimentary rocks*: 634 p., Prentice-Hall, Inc. (Englewood Cliffs, N. J.).
- Bolz, H., 1971, *Late Triassic Bairdiidae and Healdiidae*: in Paleocologie des Ostracodes, H. J. Oertli (ed.), Centre Rech., Pau, Bull., v. 5 (suppl.), p. 717-746, pl. 1-4, Société Nationale des Pétroles d'Aquitaine (Pau).
- Cadot, H. M., Jr., 1974, *Magnesium content of calcite in carapaces of benthic marine Ostracoda*: Ph.D. thesis, University of Kansas (Lawrence), 111 p. (unpubl.).
- , Van Schmus, W. R., & Kaesler, R. L., 1972, *Magnesium in calcite of marine Ostracoda*: Geol. Soc. America, Bull., v. 83, p. 3519-3522.
- , Kaesler, R. L., & Van Schmus, W. R., 1975, *Application of the electron microprobe analyzer to the study of the ostracode carapace*: Bull. Am. Paleontology, v. 65, p. 577-585.
- Chave, K. E., 1954, *Aspects of biogeochemistry of magnesium. 1. Calcareous marine organisms*: Jour. Geology, v. 62, p. 266-283.
- Clarke, R. W., & Wheeler, W. C., 1922, *The inorganic constituents of marine invertebrates*: U. S. Geol. Survey, Prof. Paper, v. 124, p. 1-56.
- Cloud, P. E., Jr., 1965, *Carbonate precipitation and dissolution in the marine environment*: in Chemical oceanography, J. P. Riley & G. Skirrow (eds.), v. 2, p. 127-158, Acad. Press (New York).
- Crisp, E. L., 1972, *Salinity, species, and age effect on the trace chemistry of nine molluscan species*: Geol. Soc. America, Abstracts with Programs, v. 4, p. 716-717. (Abstr.)
- Davies, T. T., Crenshaw, M. E. & Heatfield, B. M., 1972, *The effect of temperature on the chemistry and structure of echinoid spine regeneration*: Jour. Paleontology, v. 46, p. 874-883.
- Dodd, J. R., 1967, *Magnesium and strontium in calcareous skeletons: A review*: Jour. Paleontology, v. 41, p. 1313-1329.
- Durazzi, J. T., 1973, *Magnesium, strontium, and oxygen isotopes in the shells of ostracods*: Geol. Soc. America, Abstracts with Programs, v. 5, no. 7, p. 606. (Abstr.)
- Friedman, G. M., 1965, *Occurrence and stability relationships of aragonite, high-magnesium calcite and low-magnesium calcite under deep-sea conditions*: Geol. Soc. America, Bull. 76, p. 1191-1195.
- , Amiel, A. J., & Schneidermann, Nahum, 1974, *Submarine cementation in reefs. Example from the Red Sea*: Jour. Sed. Petrology, v. 44, p. 816-825.
- Land, L. S., 1967, *Diagenesis of skeletal carbonates*: Jour. Sed. Petrology, v. 37, p. 914-930.
- Lippman, F., 1973, *Sedimentary carbonate minerals: Minerals, rocks, and inorganic materials* 6: 228 p., Springer-Verlag (New York).
- Lipps, J. H., & Ribbe, P. H., 1967, *Electron-probe microanalysis of planktonic Foraminifera*: Jour. Paleontology, v. 41, p. 492-496.
- Loranger, D. M., 1971, *Ostracods, trace elements and Frasnian reefs in Sturgeon Lake area*: in Paleocologie des Ostracodes, H. J. Oertli (ed.), Centre Rech., Pau, Bull., v. 5 (suppl.), p. 769-786, Société Nationale des Pétroles d'Aquitaine (Pau).
- Lowenstam, H. A., 1963, *Biological problems relating to the composition and diagenesis of sediments*: in The earth sciences, T. W. Donnelly (ed.), Problems and progress in current research, Rice University Semi-centennial Pub., p. 137-195, Chicago Univ. Press (Chicago, Ill.).
- MacQueen, R. W., Ghent, E. D., & Davies, G. R., 1974, *Magnesium distribution in living and fossil specimens of the echinoid Peronella Lesueuri Agassiz, Shark Bay, Western Australia*: Jour. Sed. Petrology, v. 44, p. 60-69.
- Maddocks, R. F., 1972, *Two new living species of Saipanetta (Ostracoda, Podocopida)*: Crustaceana, v. 13, p. 28-42.
- Milliman, J. D., 1974, *Recent sedimentary carbonates*: 375 p., Springer-Verlag (New York).
- , Gastner, Manfred, & Müller, Jens, 1971, *Utilization of magnesium in coralline algae*: Geol. Soc. America, Bull. 82, p. 573-580.
- Moberly, Ralph, Jr., 1968, *Composition of mg-calcite of algae and pelecypods by electron microprobe analysis*: Sedimentology, v. 11, p. 61-82.—1973, *Rapid chamber-filling growth of marine aragonite and mg-calcite*: Jour. Sed. Petrology, v. 43, p. 634-635.
- Moore, R. C., 1961, *Treatise on invertebrate paleontology, Part Q, Arthropoda 3, Crustacea, Ostracoda*: 442 p., 334 text-fig., Geol. Soc. America, and Univ. of Kansas Press (Boulder, Colo.; Lawrence, Kans.).
- Morkhoven, F. P. C. M. Van, 1962, *Post-Paleozoic Ostracoda. Their morphology, taxonomy, and economic use. 1*: 204 p., Elsevier Publ. Co. (Amsterdam).

- Passano, L. M., 1960, *Molting and its control*: in *Physiology of Crustacea 1*, T. H. Waterman (ed.), p. 473-536, Academic Press (New York).
- Plummer, L. N., & McKenzie, F. T., 1972, *Predicting mineral solubility from rate data: Application of the dissolution of magnesium calcites*: *Geol. Soc. America, Abstracts with Programs*, v. 4, no. 7, p. 629-630. (Abstr.)
- Ponder, R. W., & Glendenning, I. G., 1974, *The magnesium content of some miliolacean Foraminifera in relation to their ecology and classification*: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 15, p. 29-32.
- Revelle, R., & Fairbridge, R. W., 1957, *Carbonates and carbon dioxide*: in *Treatise on marine ecology*, J. W. Hedgpeth (ed.), *Geol. Soc. America, Mem.* 67, v. 1, p. 239-296 (Boulder, Colo.).
- Siegel, Sidney, 1956, *Nonparametric statistics for the behavioral sciences*: 312 p., McGraw-Hill Book Co., Inc. (New York).
- Schroeder, J. H., 1969, *Experimental dissolution of calcium, magnesium, and strontium from recent biogenic carbonates: A model of diagenesis*: *Jour. Sed. Petrology*, v. 39, p. 1057-1073.
- Sokal, R. R., & Rohlf, F. J., 1969, *Biometry*: 776 p., W. H. Freeman & Co. (San Francisco).
- Weber, J. N., 1969, *The incorporation of magnesium into skeletal calcites of echinoderms*: *Am. Jour. Science*, v. 267, p. 537-566.—1973, *Temperature dependence of magnesium in echinoid and asteroid skeletal calcite: A reinterpretation of its significance*: *Jour. Geology*, v. 81, p. 543-556.
- Wolfe, K. H., Chilingar, G. V., & Beales, F. W., 1967, *Elemental composition of carbonate skeletons, minerals, and sediments*: in *Carbonate rocks*, G. V. Chilingar, H. J. Bissell, & R. W. Fairbridge (eds.), p. 23-150, B. Elsevier (Amsterdam).

H. Meade Cadot, Jr.
The Harris Center for
Conservation Education
Hancock, New Hampshire 03449

Roger L. Kaesler
Department of Geology and
Museum of Invertebrate Paleontology
The University of Kansas
Lawrence, Kansas 66045